

Age and Growth of Vermilion Snapper from the Southeastern United States

JENNIFER C. POTTS,* CHARLES S. MANOOCH III, AND
DOUGLAS S. VAUGHAN

National Marine Fisheries Service

Southeast Fisheries Science Center, Beaufort Laboratory

101 Pivers Island Road, Beaufort, North Carolina 28516-9722, USA

Abstract.—A comprehensive aging study of vermillion snapper, *Rhomboplites aurorubens*, was conducted, using 1,465 otoliths collected between 1991 and 1995 from the commercial and headboat fisheries from North Carolina through the Florida Keys. An additional 19 otoliths came from fishery-independent samples from the South Atlantic Bight for fish smaller than 254 mm total length (TL), which is the legal size limit. Marginal increment analysis revealed that rings on the otoliths were deposited annually. This observation is further substantiated by the increasing modal radius of each age ring corresponding to the increasing modal size of the fish at age. Observed ages ranged from age 1 (202 mm mean TL) to age 14 (535 mm TL). The largest fish was 600 mm TL and was estimated to be age 13. The weight–length relationship was described by the equation: $W = 9.55 \times 10^{-9}(L)^{3.04}$, where W = whole weight in kilograms and L = total length in millimeters. The von Bertalanffy equation was estimated using the inverse, weighted, back-calculated lengths at the last annulus. The equation was $L_t = 650(1 - e^{-0.144(t+0.238)})$, where t is age in years.

The vermillion snapper, *Rhomboplites aurorubens*, a small- to moderate-sized reef fish, is the most frequently caught snapper along the southeastern United States (Manooch 1984). Vermilion snapper makes a significant economic contribution to both the commercial and recreational fisheries for reef fish, and it consistently ranks among the top 12 species in dollar value of all finfish landed on the southern U.S. Atlantic coast (National Marine Fisheries Service, General Canvass data, Miami, Florida). In the western Atlantic Ocean, it occurs from North Carolina and Bermuda through the Caribbean Sea and Gulf of Mexico to southeastern Brazil (Böhlke and Chaplin 1968). The vermillion snapper is a warm-temperate to tropical species and is dominant in the mid-shelf zone (18–55 m deep) south of Cape Fear, North Carolina (Mahmoudi 1985). Off the southeastern United States it increases in relative abundance from northern Onslow Bay, North Carolina, south to northern Florida (Manooch 1984). The vermillion snapper is an indeterminate spawner from April through September (Grimes and Huntsman 1980; Cuellar et al. 1996).

Several age and growth studies of vermillion snapper from the southern U.S. Atlantic Coast and Gulf of Mexico have been conducted. Grimes (1978) collected specimens from North Carolina and South Carolina and compared scales with

whole otoliths as aging structures, noting that age determination in some older fish was difficult. Collins and Pinckney (1988) conducted an age-at-maturity study of vermillion snapper collected from Cape Fear, North Carolina, to Jacksonville, Florida. Using acetate impressions of scales, they found only 43.9% of the scales examined were legible for assigning ages, and all of these were from age-1 and age-2 fish. Examination of high resolution photographs of whole otoliths from vermillion snapper collected off northwest Florida and Texas failed to establish that growth zones on the otoliths were deposited annually (Barber 1989). More recently, Zhao et al. (1997) determined ages of mostly small vermillion snapper collected from North Carolina to Cape Canaveral, Florida, with the bulk (80%) coming from South Carolina. They successfully validated the annual deposition of opaque zones on sectioned otoliths, but the size range of their fish was limited.

Our study responds to Schirripa (1992) who pointed out the need to review aging methods and growth estimates for vermillion snapper because of the variability among studies. Our objectives were to validate aging and provide growth information for the vermillion snapper from the southeastern U.S. to be used in a subsequent stock assessment.

Methods

Otoliths of vermillion snapper were collected between 1991 and 1995 from recreational headboats

* Corresponding author: jpotts@hatteras.bea.nmfs.gov

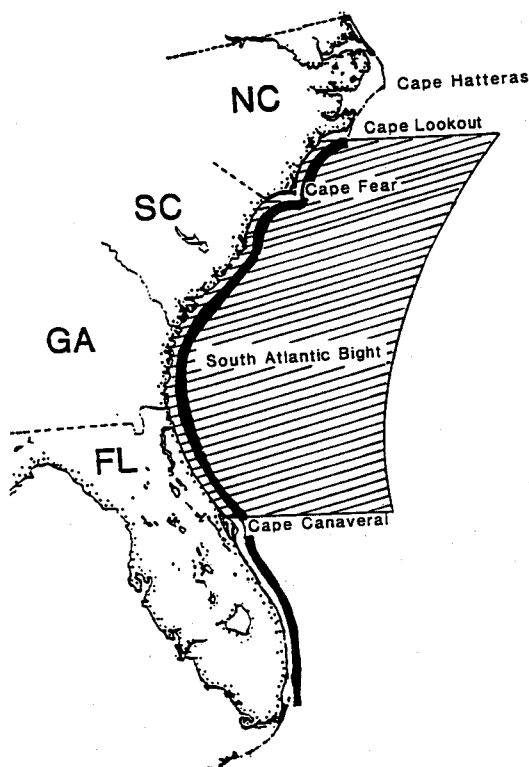


FIGURE 1.—Map of the southeastern U.S. and South Atlantic Bight (hatched area). The dark line along the coast denotes where samples for this study were taken.

and commercial hook-and-line catches from Cape Hatteras, North Carolina, through the Florida Keys (Figure 1). South Carolina Department of Natural Resources MARMAP (Marine Resources Monitoring, Assessment, and Prediction) personnel made additional independent collections using, primarily, traps and trawls. Fish were weighed (grams) and measured for total length (TL; millimeters). Sagittal otoliths were extracted through the operculum by following the methods of Manooch and Mason (1984) and Smale and Punt (1991) to minimize disfigurement of fish destined for market. The otoliths were stored dry in coin envelopes; area and date of capture were recorded on the envelopes.

The otolith collection was divided into five groups: (1) fishery-independent samples primarily from off the South Carolina Coast; (2) North Carolina and South Carolina commercial; (3) North Carolina and South Carolina recreational; (4) Florida commercial; and (5) Florida recreational. Target sample size for each group was 40 fish per 25-

mm-TL interval. Intervals with over 40 samples were randomly sampled for the target value.

From preliminary examination of whole and thin-sectioned sagittae, we determined that a transverse (dorsoventral) cut through the primordium would provide the best section. The section was ground on a precision grinder (240-mesh wheel) to 0.50 mm thickness, then polished with 1,200-grit wet and dry sandpaper and 0.1- μ m alumina-grit paste to remove scratches left by the grinder (Cowan et al. 1995).

Sections were immersed in clove oil and viewed with an image-analysis system consisting of a personal computer and video monitor and camera equipment connected to a dissecting microscope that used reflected light. We made measurements from the primordium of the otolith section to each successive opaque zone and to the edge of the otolith on the lateral surface. For preliminary analysis, opaque zones were hypothesized to be deposited annually.

Two methods were used to determine the timing of the opaque zone deposition: the mean marginal increment (distance from last annulus to the edge of the aging structure) was plotted against month of capture, and frequency distributions of the measurement from the primordium to each ring were plotted for each age.

The weight-length relationship was determined by a linear regression of \log_e -transformed values, which was transformed to $W = aL^b$, adjusting for the bias with $\frac{1}{2}$ MSE (mean squared error); W = whole weight in kilograms, and L = total length in millimeters.

The fish length-otolith radius relationship was described by regressing the log-transformed fish length on log-transformed otolith radius (R_C). Back-calculated total lengths at each age were determined using the log-transformed, otolith proportional equation (Carlander 1981; Johnson et al. 1994):

$$L_A = \exp[a + (\log_e L_C - a) \cdot (\log_e R_A / \log_e R_C) + \text{MSE}/2];$$

L_A = back-calculated length to annulus A,

a = intercept from the log-transformed total length-otolith radius regression,

L_C = total length at capture C,

R_A = otolith radius to annulus A,

R_C = total otolith radius at capture, and

MSE = mean square error (σ^2) from regression used to correct for the transformation bias.

TABLE 1.—Numbers of vermilion snapper otoliths collected, processed, and aged.

Fishery and otolith category	Source ^a				Total
	NC	SC	FL	Un-known	
Commercial					
Collected	180	70	337		587
Processed	177	64	337		578
Aged	164	61	296		521
Headboat					
Collected	285	240	352	1	878
Processed	285	217	240	1	743
Aged	216	190	223	1	630
Independent					
Collected		19			19
Processed		19			19
Aged		19			19

^a North Carolina (NC), South Carolina (SC), and Florida (FL).

Back-calculated data were used to test for Lee's phenomenon (Ricker 1969). The distance from the primordium to the first opaque zone (A1) was regressed on age. If the slope of the line was significantly different from zero, then size-selective mortality (i.e., Lee's phenomenon) or the reverse was assumed present. The regression was also performed on the second and third opaque zones to ascertain whether the pattern was consistent for the first few years of growth.

The mean back-calculated lengths from the last annulus (e.g., Vaughan and Burton 1994), inversely weighted by the sample size at each age, were used to fit the von Bertalanffy growth equation, $L_t = L\{1 - \exp[-K(t - t_0)]\}$, with the Marquardt algorithm for iterative nonlinear regression (e.g., Vaughan and Kanciruk 1982).

Differences in growth among the regions and fisheries were tested for ages 2–9 using a general linear model, repeated measures option (SAS Institute 1987), on the measurement between the primordium and the last annulus.

Finally, observed age at length was used to derive an age-length key based on the biological birth date (Manooch and Potts 1997), whereby length-frequency distributions can be converted to age-frequency distributions. Each aged fish was assigned to a 25-mm size-class interval. The age distribution was then identified as the percent of each age-per-size interval.

Results

We collected otoliths from 1,465 vermilion snapper from the headboat and commercial fisheries from North Carolina to the Florida keys and 19 from fish (<250 mm TL) collected by MAR-

TABLE 2.—Observed total lengths at age for vermilion snapper from the U.S. south Atlantic (all regions and fisheries combined).

Age	N	Total length (mm)		
		Mean	SD	Range
1	5	202	12	188–215
2	45	228	39	186–340
3	321	275	43	190–385
4	319	318	41	215–445
5	188	357	47	242–465
6	101	401	51	262–526
7	99	447	52	292–545
8	49	492	34	402–547
9	23	523	23	463–560
10	9	521	28	477–562
11	4	530	25	506–563
12	3	568	24	545–593
13	3	593	7	585–600
14	1	535		

MAP within the South Atlantic Bight (Table 1; Figure 1). The latter supplemented the fishery-dependent samples because these smaller fish were not retained by the recreational and commercial fishermen after 1991 when the 254-mm (10-in) size limit was established. The lengths of all fish examined ranged from 186 to 600 mm TL (Table 2).

Otoliths showed alternating wide translucent zones and narrow opaque zones that made continuous orbits around the primordium (Figure 2). Age was estimated by counting the opaque zones. Some otoliths exhibited check marks (also noted by Zhao et al. 1997), but those marks did not make continuous orbits around the entire section.

Eighty-seven percent of the otolith sections were legible ($N = 1,170$), and the estimated ages ranged from 1 to 14 years. The oldest fish (age 14) measured 535 mm TL; the largest fish (600 mm TL) was estimated to be age 13 and was taken by the commercial fishery (Table 2).

Marginal increments for ages 1–3 were minimal in June (Figure 3), suggesting the opaque zones formed once per year. Additionally, a frequency distribution of the measurements from the otolith primordium to successive rings exhibited consistent modes for each age (Figure 4). The increasing modal radius corresponded well with increasing modal size of fish at age. Increasing overlap of the distributions and decreasing increment length (distance between each ring) as age increased were consistent with the slowing of somatic growth and the shortened distance between rings on the edge of the otolith. This relationship is consistent with the hypothesis that bands are deposited annually.



FIGURE 2.—Photograph of transverse section of a vermilion snapper sagittal otolith. The line denotes the plane of measurement on the dorsal side of the section from the focus to each annulus and the edge. The cross hairs show where the annuli were measured (outer edge of the thin opaque zone), and the arrows indicate check marks within the annulus.

Total fish weights were available for 443 vermilion snapper ranging from 186 to 545 mm TL and 0.67 to 2.22 kg. The best-fit equation for these length-weight data was $W = 9.55 \times 10^{-9}(L)^{3.04}$ ($r^2 = 0.95$ and $MSE = 0.026$).

The fish length (L_C)–otolith radius (R_C) relationship for vermilion snapper was best described by the \log_e – \log_e transformed data, where $L_C = 3.85 \times 10^{-3}(R_C)^{1.41}$ ($N = 1,143$, $r^2 = 0.74$, $MSE = 0.02$). All data were used to back-calculate

lengths at age from the otolith proportional equation: $TL = \exp[-5.57 + (\log_e L_C + 5.57) \cdot (\log_e R_A / \log_e R_C) + 0.016/2]$. We calculated the mean length of vermilion snapper at the time of each annulus formation and the mean annual growth increment at each age (Table 3).

Size-selective mortality (Lee's phenomenon) was evident for vermilion snapper in the southeastern U.S. fishery, but it probably has a negligible effect in interpreting growth patterns. The linear regression of the measurement of the first annulus (A1) on age of fish has a positive slope significantly different from zero ($N = 966$, $r^2 = 0.01$, $P = 0.0027$). The low significant r^2 value, which resulted from the large sample size, allowed the test to detect subtle levels of Lee's phenomenon. This trend continued into the second annulus and the third annulus at the $P < 0.05$ level with r^2 values of 0.03 and 0.04, respectively. However, the explanatory ability of these regressions is extremely small.

The test on the growth rates of the vermilion snapper between regions and fisheries (Figure 5) was unable to detect any consistent pattern of differences. Therefore, growth of vermilion snapper throughout the southeastern U.S. is best represented by the equation $L_t = 650(1 - e^{-0.144(t+0.238)})$; $N = 983$.

The vermilion snapper age-length key (Table 4) is presented in 25-mm length intervals (i.e., 175 mm includes fish 175–199 mm long); the number of fish in each length-class at each age is given

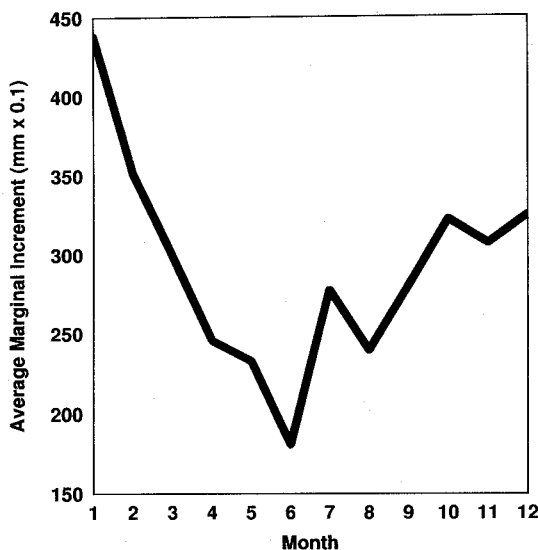


FIGURE 3.—Marginal increment analysis for the vermilion snapper from the southeastern U.S. Ages 1–3 were used in the analysis ($N = 321$).

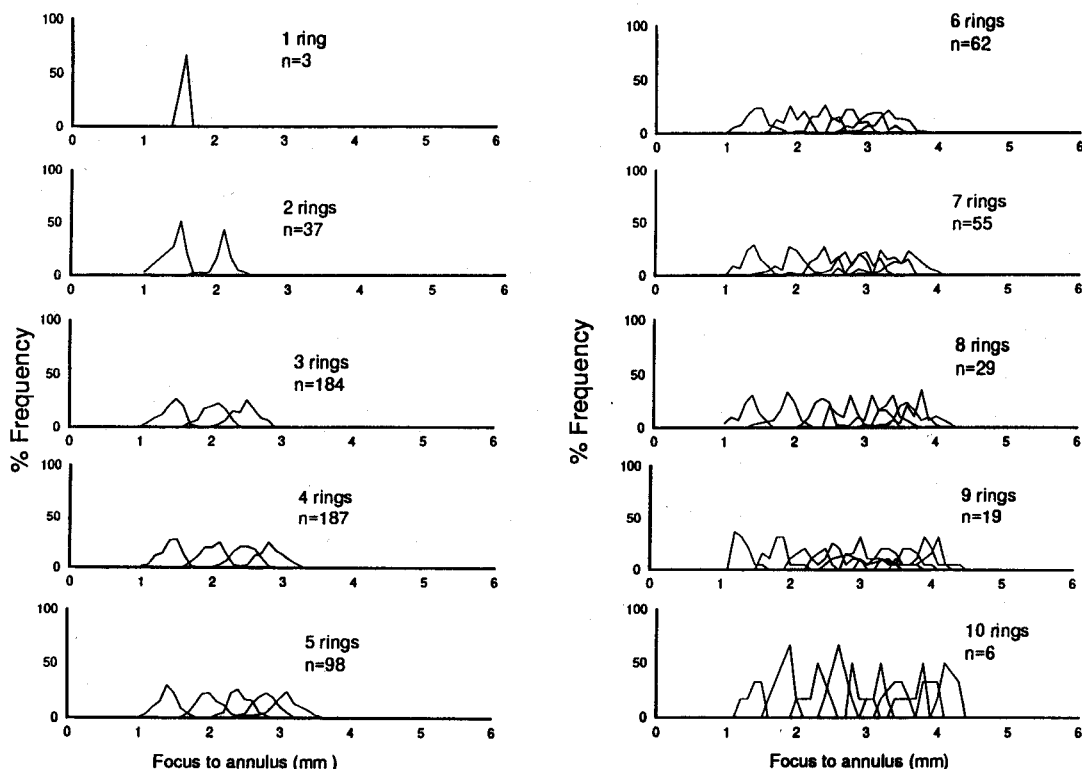


FIGURE 4.—Frequency distribution of the ring measurements to each annulus by age for the vermilion snapper from the southeastern U.S.

along with the corresponding percentage of total fish in the length-class at each age.

Discussion

In this study, we used marginal increment analysis and sectioned otoliths to validate the aging of vermilion snapper. Annuli are deposited on the otoliths in June, which is consistent with the findings in Zhao et al. (1997). Another snapper, the red snapper *Lutjanus campechanus*, deposits its annular rings on sagittae during the same period (Nelson and Manooch 1982; Manooch and Potts 1997).

Limited circumstantial evidence suggests that the first annular ring on vermilion snapper otoliths may be related to onset of first spawning. Cuellar et al. (1996) found mature vermilion snapper at 186 mm TL, and the smallest specimen in this study, 188 mm TL, was estimated to be age 1. Because June is the peak of vermilion snapper spawning (Cuellar et al. 1996), we suspect that the formation of the annular ring may be associated with spawning, as was suggested by Grimes (1978) and Zhao et al. (1997).

Our study was comprehensive because specimens were collected from the recreational and commercial hook-and-line fisheries from North Carolina to the Florida Keys. Also, to compensate for low sample size of fish smaller than 250 mm TL (i.e., fish not retained due to size-limit regulations), fishery-independent samples of small fish were collected. The asymptotic total length for vermilion snapper in our study is similar to that (627 mm) estimated by Grimes (1978), but the growth rates are different (our study: $K = 0.144$; Grimes: $K = 0.198$; compare curves in Figure 5). This could be attributed to older ages being underestimated in Grimes' study because scales and whole otoliths were used. Moreover, Grimes estimated the von Bertalanffy parameters using all the back-calculated data with no weighting scheme.

The estimated growth curve from this study was most comparable to Zhao et al.'s (1997) curve for 1979–1981 (Figure 5): $L_t = 562(1 - e^{-0.202(t+0.117)})$. This similarity may be due to Zhao et al.'s samples coming mostly (66%) from hook-and-line samples, yet their later two sampling periods (1982–

TABLE 3.—Mean observed total lengths (TL, mm) and back-calculated lengths at age (year) for vermillion snapper from the southern U.S. Atlantic coast.

Observed			Back-calculated TL (±SE) at age:													
Age	Mean TL (±SD)	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	202 (11.6)	4	133 (3)													
2	228 (39.3)	43	118 (3)	193 (4)												
3	275 (43.3)	292	111 (1)	181 (2)	241 (2)											
4	318 (41.3)	277	110 (1)	178 (1)	239 (2)	290 (2)										
5	357 (46.8)	153	112 (2)	180 (2)	237 (2)	287 (3)	331 (4)									
6	401 (51.1)	81	113 (2)	178 (3)	236 (3)	288 (4)	337 (5)	378 (6)								
7	447 (51.6)	69	114 (2)	182 (3)	240 (4)	292 (4)	340 (5)	384 (6)	423 (6)							
8	492 (33.9)	33	111 (2)	180 (3)	242 (3)	294 (4)	342 (5)	389 (5)	431 (6)	471 (6)						
9	523 (22.9)	19	107 (3)	169 (3)	230 (4)	283 (4)	334 (5)	381 (5)	426 (5)	470 (5)	509 (6)					
10	521 (28.3)	6	108 (3)	164 (7)	215 (7)	258 (6)	301 (5)	336 (7)	379 (9)	417 (10)	457 (9)	495 (9)				
11	530 (24.7)	3	114 (3)	178 (11)	238 (19)	286 (28)	333 (27)	371 (26)	405 (29)	442 (26)	424 (65)	499 (18)	521 (19)			
12	568 (24.1)	2	105 (8)	156 (2)	209 (2)	248 (6)	294 (6)	337 (5)	374 (4)	410 (8)	453 (12)	493 (11)	524 (6)	561 (14)		
13	593 (7.5)	1	96	164	222	282	321	364	407	433	467	490	520	550	565	
14	535	1														535
All		983														
Weighted mean TL			112	180	239	289	334	380	423	462	486	495	521	558	565	535
Increment			112	68	59	50	45	46	43	39	24	9	26	37	7	−30

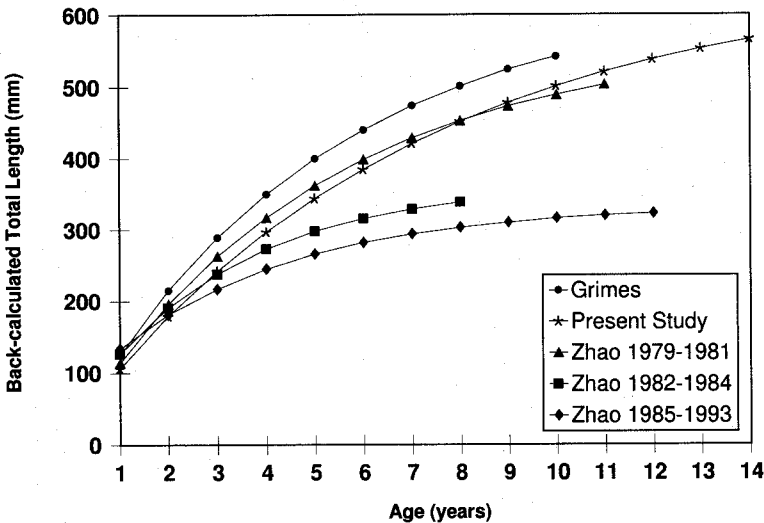


FIGURE 5.—Comparison of theoretical growth curves for vermillion snapper from the southeastern U.S. (present study), from North Carolina and South Carolina (Grimes 1978), and from the South Atlantic Bight for three time periods (Zhao et al. 1997).

TABLE 4.—Age–total length key of the vermilion snapper collected from the southern U.S. Atlantic coast. Whole numbers are numbers of fish in the length-group assigned to the given age-class; percent of fish in the length-group is given in parentheses.

Total length ^a (mm)	Age-class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
175	2 (10.5)	14 (73.7)	3 (15.8)											
200	3 (5.4)	11 (19.6)	40 (71.4)	2 (3.6)										
225		8 (8.9)	62 (68.9)	19 (21.1)	1 (1.1)									
250		5 (5.0)	52 (51.5)	32 (31.7)	11 (10.9)	1 (1.0)								
275		4 (3.1)	52 (40.6)	51 (39.8)	15 (11.7)	5 (3.9)	1 (0.8)							
300		1 (0.7)	70 (46.4)	60 (39.7)	16 (10.6)	1 (0.7)	3 (2.0)							
325		2 (1.3)	28 (17.7)	88 (55.7)	31 (19.6)	6 (3.8)	3 (1.9)							
350			12 (10.2)	45 (38.1)	44 (37.3)	15 (12.7)	2 (1.7)							
375			2 (2.6)	13 (16.9)	40 (52.0)	17 (22.1)	5 (6.5)							
400				6 (10.5)	16 (28.1)	19 (33.3)	15 (26.3)	1 (1.8)						
425				2 (3.8)	10 (18.9)	22 (41.5)	15 (28.3)	4 (7.6)						
450					5 (10.4)	10 (20.8)	23 (47.9)	9 (18.8)	1 (2.1)					
475						3 (7.7)	18 (46.2)	14 (35.9)	2 (5.1)	2 (5.1)				
500						1 (3.1)	9 (28.1)	11 (34.4)	7 (21.9)	2 (6.3)	2 (6.3)			
525						1 (3.0)	5 (15.2)	10 (30.3)	10 (30.3)	4 (12.1)	1 (3.0)	1 (3.0)		1 (3.0)
550									3 (50.0)	1 (16.7)	1 (16.7)	1 (16.7)		
575												1 (33.3)	2 (66.7)	
600													1 (100.0)	

^a Lengths given are the lower limit of a 25-mm length interval, thus 175 mm includes fish 175–199 mm long, 200 mm includes fish 200–224 mm, etc.

1984 and 1985–1993) contained many smaller fish that came primarily from trap (67%) and trawl (76%) samples. Because of the large number of small fish and the limited range of larger fish, values of L_{∞} from these two later periods were only about half of the maximum observed length in the commercial fishery (1982–1984: $L_{\infty} = 365$; 1985–1993: $L_{\infty} = 333$). In fact, 50% of the samples from our study were larger than the L_{∞} predicted by Zhao et al. for 1985–1993.

Zhao et al. (1997) argue that the dramatic decrease in L_{∞} and size-at-age from 1979 to 1993 is due either to the population being “fished down,” making the larger individuals relatively less numerous, or to the mechanism of intense selective fishing for faster growing fish, which resulted in

shifting the genotype to one with lower growth potential. They also contend that the gear used to collect the samples for their study was not size selective (i.e., no gear bias). Our study suggests that gear bias may be important. Other researchers demonstrate size-selectivity and age-selectivity of various gear types (Rollefsen 1953; Punt et al. 1996). Ranges of fish size and age in aging studies may influence the estimates of the von Bertalanffy growth equation if they are not representative of the population (Goodyear 1995). Our estimates of the growth rate and L_{∞} are comparable to the ones found by Grimes (1978) and Zhao et al. (1997) in the earliest period (primary gear for all was hook and line). Zhao et al. shifted gear emphasis from hook and line in the 1979–1981 period to traps

and trawls in the later two periods, and we believe the size-at-age and values of L_{∞} and K reflect that shift. The maximum observed length in our study was 600 mm, whereas their maximum observed length from their latest period was only 426 mm. The dramatic decrease (35%) in L_{∞} from Zhao et al.'s 1982–1984 data comes within 2 years of the first period, although there is only a 6% decrease between the 1982–1984 and 1985–1993 periods. The 35% decrease is highly improbable if it is attributed to “fishing down” or to a genetic shift in the population to favor slower growing individuals, as Zhao et al. suggest. We maintain that the different results presented in their study were caused by gear bias, not by fishing pressure. Hook-and-line gear is less size-selective than traps and trawls because even small vermilion snapper have large enough mouths to readily take hook-and-line bait. We do not believe that the fisheries catch only the fastest growing individuals, and the wide variation in size-at-age (Table 4) from our study supports that hypothesis.

The red snapper, another heavily exploited reef fish, was also recently re-aged (Manooch and Potts 1997). The first age-and-growth study (Nelson and Manooch 1982) used samples from the late 1970s, whereas the updated study used samples from the 1990s. The size-at-age did not change and the von Bertalanffy parameters were almost identical. If red snapper, which lives to 25 years and starts spawning at age-2, does not show a decrease in size-at-age attributable to intensive fishing pressure, one must wonder why vermilion snapper would show such a dramatic decrease over the same time period, as Zhao et al. propose.

We believe that the von Bertalanffy parameters from our study are most representative of the vermilion snapper population from the southeastern United States and that our study lays the groundwork for a subsequent stock assessment of the species.

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